



***AEGILOPS AUCHERI* BOISS. — ALMOST FORGOTTEN AS A SEPARATE SPECIES — MAY ALSO BE REGARDED AS RATHER CLOSE TO A PROBABLE ANCIENT DONOR OF SUBGENOME G FOR POLYPLOID WHEATS OF THE TIMOPHEEVII-ZHUKOVSKIY LINEAGE**

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Resume

From the time of Theophrastus, for two millennia, many plants have been considered an herb liked by goats and called aegilops. This had continued until the introduction of binary nomenclature by C.Linnaeus when he described the genus *Aegilops* L. This article contains excerpts from modern and historical classifications of the genus *Aegilops* as compiled by various authors through the years, but the emphasis is on *Aegilops* species from the section Sitopsis. Nowadays, there is some mixing between the *Aegilops* classifications proposed in the late 1920s. One of them was developed by P.M.Zhukovsky and had a section called Sitopsis, and another classification was developed by A.Eig, where this section was called Platystachyum but was divided into two subsections (Emarginata and Truncata), both of which are now within the generally accepted modern section Sitopsis. Numerous renamings of *Aegilops* species from the section Sitopsis during more than 2 centuries were noted. The interest in the section Sitopsis of the genus *Aegilops* is due to the fact that its species are potential donors of subgenomes of polyploid wheats. Polyploid wheats constitute two lineages (Emmer and Timopheevii) with the genomic formulae BA, BAD, GA, GAA. The greatest doubts are raised by the first maternal subgenomes of these lines (B and G), the donor of which was some species of the section Sitopsis during the initial crossing with diploid wheat. A comparison of nucleotide sequences of complete chloroplast genomes of species from the *Triticum–Aegilops* alliance clearly indicates that species from the subsection Emarginata could not be this donor. The most likely donor of subgenomes B and G was either *Ae. speltoides* or a closely related species (from the subsection Truncata) that has not yet been found or is already extinct. Formerly, this section has included such species as *Ae. aucheri*, which is currently considered to be *Ae. speltoides* or its subspecies — merely its synonym — but which had probably been unreasonably rejected as an independent species by a substantial number of taxonomists in the second half of the 20th century. Sequencing of the complete plastid genome of this species from seven specimens of different geographical origin shows that it diverges from *Ae. speltoides*. The phylogenetic tree constructed on the basis of a comparison of genomes of diploid wheats, *Aegilops* from the subsection Emarginata, *Ae. tauschii*, *Ae. aucheri*, *Ae. speltoides*, and polyploid wheats of two lineages (turgidum-aestivum and timopheevii-zhukovskiyi) indicates that *Ae. aucheri* can also be considered a potential donor of subgenome G for timopheevii-zhukovskiyi wheats, whereas turgidum-aestivum wheats are distant from the other species.

Keywords: *Aegilops*, *Aegilops aucheri*, *Ae. speltoides*, section Sitopsis, subsection Truncata, subsection Emarginata, classification, donor, subgenome G, polyploid wheats, *Triticum*, Emmer lineage, Timopheevii lineage, phylogenetic tree, whole genome sequencing

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Introduction

Hexaploid wheat *Triticum aestivum* L. is the most important cereal crop, and it is not surprising that there is much interest in its relatives, both cultivated and wild, including donors of their subgenomes. Polyploid wheats form two lineages — Emmer (turgidum-aestivum) and Timopheevii (timopheevii-zhukovskyi) — with genomic formulae for tetraploids and hexaploids: BA, BAD and GA, GAA, respectively. For the third subgenomes of hexaploids (D and A) donors are known: with high probability, these are diploid *Aegilops tauschii* Coss. and diploid wheat *T. monococcum* L., respectively. The second subgenomes of both lineages have been derived either from diploid wheat *T. urartu* or from related species that have not yet been identified or are extinct. A large number of articles and reviews, including our own [Vakhitov et al., 2003; Kuluev et al., 2023], are devoted to these issues, but the origin of the second and third subgenomes of polyploid wheats will not be addressed here because our focus is on the species that became maternal forms at the first crossing between diploid wheat and *Aegilops* during the creation of a primary tetraploid. Thus, the first subgenomes (B and G) of these lineages have most likely been derived either from diploid *Ae. speltoides* of the section Sitopsis, subsection Truncata, or from related species that have not yet been identified or are also already extinct. This is what is generally thought, although some articles refute this notion [see review by Haider, 2013]. It should be emphasized that in 1929, in crossing experiments with tetraploid wheat *T. turgidum* and diploid *Ae. speltoides* (serving as the paternal form), it was suggested for the first time that this species could be a donor of one of the two subgenomes of tetraploid wheat, on the basis of the discovery of seven bivalents and seven univalents [Jenkins, 1929]. Later, based on the knowledge that subgenome A derives from diploid wheat, it has been proposed that *Ae. speltoides* is a donor of subgenome B via an analysis of metaphase chromosomes and positions of nucleoli [Pathak, 1940]. On the other hand, there is another *Aegilops* species that can also be regarded as a potential donor of G and even B subgenomes. This is *Ae. aucheri* Boiss., which will receive special attention in this article.

Goat's grasses

Theophrastus mentioned aegilops (αἰγίλωψ) several times in Liber 8 (chapters 7 and 9) of his “De Historia Plantarum” some 2300 years ago, in the first case, stating that this plant appears in spring. In ancient Greek, aegilops can be interpreted as “an herb liked by goats.” This explains why, for two millennia, the name *Aegilops* has referred to a number of herbaceous plants and other plants. van Slageren [1994] devoted considerable attention to the pre-Linnaean period in the

history of the study of *Aegilops*, and therefore we will not go into this topic here. At the time, different spellings of this word were used: “Ægylops” and “Ægilops.” Names Ægylops I, Ægylops II, Ægylops III, Ægylops IV, Ægylops V, and Ægylops VI meant very different plants: aside from *Aegilops* proper, plants from genera *Bromus*, *Hordeum*, *Stipa*, *Avena*, and others from different families. In Latin, even before the binary nomenclature of Linnaeus, such phrase-names as “*Aegilops herba*” and “*Aegilops arbor*” had been used. The latter plant (oak) was renamed by C. Linnaeus in 1753 in the first volume of “*Species Plantarum*” as *Quercus Aegilops* L. (Fig. 1).

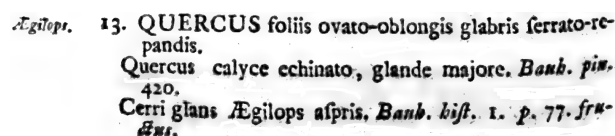


Fig. 1. An excerpt from Linnaeus’ “*Species Plantarum*” (Volume II, page 996)

In the second volume of “*Species Plantarum*” (pages 1050–1051), Linnaeus also presented five species of *Aegilops* L.: *Ae. ovata*, *Ae. caudata*, *Ae. squarrosa*, *Ae. triuncialis*, and *Ae. incurva*. The latter was excluded in the next edition. Linnaeus placed the genus *Aegilops* in Polygamia Monoecia (Fig. 2). At the same time, the closest relatives of *Aegilops*, wheat taxa (*Triticum* L.), were placed by Linnaeus in the first volume (seven species, pages 85–87) in Triandria Digynia.



Fig. 2. An excerpt from Linnaeus’ “*Species Plantarum*” (Volume II, page 1050)

Because we are interested only in representatives of the modern section Sitopsis, the examination of the remaining of *Aegilops* species ends here. In addition to the monograph by M.W. van Slageren [1994], a very detailed description of representatives of the genus *Aegilops* is given in many articles, books, and book chapters [Kilian et al., 2011; Yen, Yang, 2020; Feldman, Levy, 2023].

Section Sitopsis

Before listing the *Aegilops* species that make up the section Sitopsis, it should be noted that during the last two centuries, many botanists have made repeated attempts to unite genera *Triticum* and *Aegilops* via complete or partial absorption of the latter by the former.

Accordingly, a brief history of the discovery of different species of the genus *Aegilops* in relation to the modern section Sitopsis is outlined below.

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In 1775, P. Forsskal, exploring the flora of Egypt, described a new species, *Triticum bicornis* Forssk., now known as *Aegilops bicornis* (Forssk.) Jaub. et Spach. from Sitopsis, the subsection Emarginata. In 1837, I.F. Tausch described several species of *Aegilops*, including *Aegilops speltoides* Tausch. In 1844, P.E. Boissier described the species *Aegilops Aucheri* Boiss. and gave it a species epithet in honor of recently deceased botanist P.M.R. Aucher-Eloy, while using the latter's collections made by him in Syria near Aleppo. Later, in 1884, Boissier recorded nine species of *Aegilops*, while retaining *Ae. aucheri*. In 1846, F. Savignone described a new species, *Agropyrum tournefortii*, which turned out to be *Ae. speltoides*, but in 1848, A. Bertoloni renamed this species to *Triticum ligusticum* (Savign.) Bertol., and in 1864, this species was again renamed by E.S.-C. Cosson as *Aegilops ligustica* (Savign.) Cosson. In 1848, F. Parlatore published *Triticum aucheri* (Boiss.) Parl. in "Flora Italiana," together with the species *T. ligusticum*. In 1850–1853, H.F. Jaubert and E. Spach proposed their classification of *Aegilops*, thereby dividing this genus into six subgenera, including the subgenus *Sitopsis*, in which they included *Ae. bicornis* (Forssk.) Jaub. et Spach and *Ae. speltoides* Tausch. They named one of these subgenera (now defunct) *Uropyrum*, consisting of the single species *Ae. macrura* Jaub. et Spach, which has later been considered a variety of *Ae. speltoides* Tausch. According to Zhukovsky, however, *Ae. macrura* is the same as *Ae. aucheri* [Zhukovsky, 1928]. In 1854, D.A. Godron renamed *Ae. speltoides* as *Ae. agropyroides* Godr. In 1855, E.G. Steudel listed 32 species of *Aegilops* in "Synopsis Plantarum Graminearum"; among these species, together with some original names given to them (not fixed in the botanical literature), he mentioned *Ae. macrura*, *Ae. bicornis*, *Ae. speltoides*, *Ae. aucheri*, *Ae. agropyroides*, and *Ae. crithodium* Steud., which was actually einkorn *T. monococcum*. In 1890, K. Richter merged genera *Aegilops* and *Triticum*, while mentioning *T. ligusticum* Bertol., *T. aucheri* Parl., and *T. speltoides* Godr. among 15 species within the new taxon. C.G. Post in 1896 in his book "Flora of Syria, Palestina, and Sinai" listed eight species of *Aegilops* including *Ae. aucheri*. G.A. Schweinfurth and R.H. Muschler in 1912 described a new species from the modern section Sitopsis: *Ae. longissima* Schw. et Muschler. In 1929, A. Eig described another species: *Ae. sharonensis* Eig. Finally, in 1977, M. Feldman and M. Kislev described a new species of *Aegilops* (so far the last species in Sitopsis) — *Ae. searsii* Feld. et Kis. — which they isolated from a habitat of *Ae. longissima*.

Such a deep dive into the history of the research on *Aegilops* is provided here to demonstrate that for many years, the variety of opinions of different botanists about morphological features of the *Aegilops* specimens that they studied has been changing.

Since the late 1920s, however, some order has been established in the systematics of *Aegilops*, owing to two papers — by P.M. Zhukovsky [1928] and by A. Eig [1929] — both initiated by N.I. Vavilov. The classifications of Zhukovsky and Eig served as the basis for all subsequent classifications of *Aegilops*. More earlier classifications of the genus *Aegilops* will not be discussed here because of their small numbers of species that belong to the modern section Sitopsis.

Nowadays, on the website of Kansas State University (https://www.k-state.edu/wgrc/wheat_tax/index.html), there are several classifications of the genus *Aegilops*, both current and historical classifications. Below we provide excerpts from their tables in chronological order with our comments only on species from the modern section Sitopsis, subsection Truncata, but for the classification of Eig, the subsection Emarginata was also added.

Classification of *Aegilops* according to A. Eig 1929 -

Section Platystachys Eig

Subsection Emarginata Eig

Aegilops bicornis (Forssk.) Jaub. & Spach

var. *typica*

var. *mutica* (Asch.) Eig

Aegilops longissima Schweinf. & Muschl. in Muschl.) Eig

Aegilops sharonensis Eig

var. *typica*

var. *major* Eig

Subsection Truncata Eig

Aegilops speltoides Tausch

var. *typica*

var. *polyathera* (Boiss.) Eig

Aegilops ligustica (Savign.) Cosson

As one can see, Eig has divided the section Platystachys into two subsections: Emarginata and Truncata. Now the subsection Emarginata is composed of the following *Aegilops* species: *Ae. bicornis*, *Ae. sharonensis*, *Ae. longissima*, and *Ae. searsii*.

Classification of *Aegilops* according to P.M. Zhukovsky 1928 -

Section Sitopsis (Jaub. & Spach) Zhuk.

Aegilops aucheri Boiss.

subsp. *polyathera* Boiss.

var. *hirto-hispida* Zhuk.

var. *unicolor* Zhuk.

subsp. *virgata* Zhuk.

var. *striata* Zhuk.

var. *vellea* Zhuk.

Aegilops speltoides Tausch

subsp. *ligustica* (Savign.) Zhuk.

var. *scandens* Zhuk.

var. *muricata* Zhuk.

subsp. *submutica* Zhuk.

Nonetheless, there is currently some mixing between Zhukovsky's *Aegilops* classification, which had a section called Sitopsis (originally proposed as a

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subgenus by Jaubert and Spach), and the classification developed by Eig, where this section was named *Platystachyum* but was divided into two subsections — *Emarginata* and *Truncata* — both of which are now within the generally recognized section *Sitopsis*.

Classification of *Aegilops* according to H.Kihara 1954 -
Section *Sitopsis* (Jaub. & Spach) Zhuk.
Aegilops speltoides Tausch

It is necessary to mention that Kihara [1954] classified nine species in three groups, among them “S-group with *Ae. speltoides* (incl. *Ae. aucheri*), *bicornis* and *longissima* (incl. *sharonensis*).” Later, Kihara [1970] made an addendum to his classification, in which he listed the following species in the section *Sitopsis*: “*Ae. speltoides* Tausch. (incl. *Ae. aucheri* Boiss.), *Ae. longissima* Schwein. et Muschl. (including *Ae. sharonensis* Eig), *Ae. bicornis* (Forssk.) Jaub. et Sp.”

Reclassification of *Aegilops* according to M.S.Chennaveeraiah 1960 -
Triticum L. (only S-genome species moved into *Triticum*)
Section *Sitopsis* (Jaub. & Spach) Chennav.
Triticum speltoides (Tausch) Gren. ex K.Richter
subsp. *speltoides*
subsp. *ligusticum* (Savign.) Chennav.
subsp. *aucheri* (Boiss.) Chennav.

Classification of *Aegilops* according to K.Hammer 1980 -
Subgenus *Sitopsis* Jaub. & Spach
Aegilops speltoides Tausch
subsp. *speltoides*
var. *speltoides*
f. *speltoides*
f. *striata* (Zhuk.) K.Hammer
var. *polyathera* (Boiss.) Eig
f. *polyathera* (Boiss.) K.Hammer
f. *unicolor* (Zhuk.) K.Hammer
subsp. *ligustica* (Savign.) Zhuk.
var. *ligustica* (Savign.) Bornm.
f. *ligustica* (Savign.) K.Hammer
f. *muricata* (Zhuk.) K.Hammer

Classification of *Aegilops* according to J.R.Witcombe 1983 -
Section *Sitopsis* (Jaub. & Spach) Zhuk.
Aegilops ligustica (Savign.) Cosson
Aegilops speltoides Tausch

Reclassification of *Aegilops* according to A.Love 1984 -
Genus *Sitopsis* (Jaub. & Spach). Love
Sitopsis speltoides (Tausch). Love

Classification of *Aegilops* according to van Slageren 1994 -
Section *Sitopsis* (Jaub. & Spach) Zhuk.
Aegilops speltoides Tausch
var. *speltoides*
var. *ligustica* (Savign.) Fiori

Another Kansas State University web page
(https://www.k-state.edu/wgrc/wheat_tax/Taxonomy/compaeg.html)

contains a Comparative Classification Table of *Aegilops* names. Several *Aegilops* classifications by different authors with a comparison of species are given in the following publications too: Schneider et al. [2008] and Kilian et al. [2011].

W.M.Bowden [1959] has proposed his classification in which he once again combined genera *Aegilops* and *Triticum* into a single genus, *Triticum*, thereby leaving only four *Aegilops* species from the section *Sitopsis* (which he himself did not distinguish), including their forms: *T. bicornis* Forssk., *T. longissimum* (Schweinf. & Muschl. in Muschl.) Bowden, *T. speltoides* (Tausch) Gren. ex Richter f. *speltoides*, and *T. speltoides* (Tausch) Gren. ex Richter f. *ligusticum* (Savign.) Bowden. At the same time, Bowden noted that there were intermediates between f. *speltoides* and f. *ligusticum*.

Soviet botanist P.A.Gandilyan [1978], in his classification of species of the genus *Aegilops*, divided them into five unusual groups, as a result of which the species usually affiliated with the section *Sitopsis* ended up in different groups. *Ae. aucheri* was placed in the fourth group, while *Ae. speltoides* and *Ae. bicornis* were assigned to the fifth group. At the same time, *Ae. longissima* was simultaneously in the fourth group and fifth group.

R.L.Boguslavsky together with his colleague O.V.Golik [2004] published the book “Genus *Aegilops* L. as a Genetic Resource of Breeding” (in Russian), where they presented an *Aegilops* genus system containing *Ae. speltoides* ssp. *speltoides* and ssp. *ligustica* in the subgenus *Truncata* with a mention of their synonyms used in the modern literature. For the former subspecies, the following versions of names were given among others: *Ae. aucheri* Boiss. and *T. speltoides* ssp. *aucheri* (Boiss.) Chennav.

Ae. speltoides is present in all these classifications, including its names *Triticum speltoides* and *Sitopsis speltoides*. *Ae. aucheri* with a number of subspecies and versions of names is present only in the classifications of Zhukovsky and Gandilyan. *Aucheri* as a subspecies of *Ae. speltoides* is also present in the Chennaveeraiah classification. *Ae. ligustica* is listed as a species in the classifications of Eig and Witcombe. Furthermore, *ligustica* is included as a subspecies or variety of *Ae. speltoides* in the classifications of Zhukovsky, Chennaveeraiah, Hammer, and van Slageren.

Thus, *Ae. aucheri*, which is currently considered to be the same as *Ae. speltoides* or to simply be its synonym, had probably been mistakenly abandoned as an independent species by a number of taxonomists in the second half of the 20th century. In his monograph, Zhukovsky [1928] gave much attention to morphological description of *Ae. speltoides* and *Ae. aucheri*, and presented four groups of distinguishing characteristics for them, thereby convincingly demonstrating that they are two separate species. At that time, it was not known that

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Ae. speltoides is a potential donor of one of subgenomes of tetraploid wheats. The morphological differences between *Ae. speltoides* and *Ae. aucheri* described in detail by Zhukovsky will not be discussed here because it has become possible to use nucleotide sequence data, including complete genomes, to resolve the taxonomy of these species. This is because in terms of showing relationships between species, a comparison of nucleotide sequences is much more accurate than a comparison of externally visible morphological characteristics.

Therefore, according to some botanists, the species we are interested in, *Ae. aucheri*, is a subspecies of *Ae. speltoides*; in our opinion, this notion unjustifiably "impoverishes" the subsection *Truncata* because many specialists emphasize that the species *Ae. speltoides* is very polymorphic. For instance, it has been shown that visible morphological distinct features of *Ae. speltoides* should be considered a dimorphism of a species characterized by "two types - *speltoides* (= *aucheri*) and *ligustica*" [Zohary, Imber, 1963]. Again, nucleotide sequence data, including the complete chloroplast genome, may enable a more accurate assessment of the relationships.

***Aegilops aucheri* in different articles**

There are many articles in which *Ae. aucheri* is mentioned as a separate species or subspecies. For example, O.N.Sorokina [1928] has researched chromosomes of several *Aegilops* species, including *Ae. aucheri*, *Ae. speltoides* ssp. *ligustica*, and *Ae. speltoides* ssp. *submutica*. Other old articles had mentioned hybridization between species *Ae. speltoides* ? *Ae. aucheri* [Kihara, Lilienfeld, 1932] and *Ae. longissima* ? *Ae. aucheri* [Kihara, 1951].

Quite a few authors have investigated *Ae. aucheri* at the nucleotide and protein level, by estimating the amount of nuclear DNA, analyzing proteins, and sequencing individual fragments of the nuclear genome and plastome. For example, the nuclear DNA content was determined in many representatives of *Aegilops*, mainly from the section *Sitopsis*, including six specimens of *Ae. aucheri* [Furuta et al., 1977]. Recently, other authors estimated the nuclear DNA content in several *Aegilops* species, including specimens of *Ae. speltoides* var. *aucheri* and *Ae. speltoides* var. *ligustica* (five specimens of each) [Najafi et al., 2022]. Two-dimensional gel electrophoresis was performed to examine proteins from a number of *Triticum* and *Aegilops* species; as a result, it was concluded that the donor of the subgenome B of polyploid wheats belonging to the *turgidum-aestivum* lineage is a species closer to the *Ae. speltoides*–*Ae. aucheri* group than to any other *Aegilops* species of the section *Sitopsis* [Bahman et al., 1988].

The phylogeny of wheats has been studied by restriction fragment length polymorphism (RFLP) analysis of nuclear DNA from species of the section *Sitopsis*,

including *Ae. aucheri* as a form of *Ae. speltoides* [Sasanuma et al., 1996]. For the isolation and characterization of genome-specific DNA sequences in *Triticeae* species, one of analyzed taxa has been *Ae. speltoides* ssp. *aucheri* [Anamthawat-Jonsson, Heslop-Harrison, 1993]. Other authors have researched the chromosomal distribution of repetitive sequences by *in situ* hybridization by means of *Ae. speltoides* var. *aucheri* as a species [Belyayev et al., 2001]. J.Dvorak with coauthors mapped the locus that controls *ligustica/aucheri* spike syndrome in the centromeric region of *Ae. speltoides* chromosome 3 and demonstrated that *ligustica* is completely dominant over *aucheri* in a natural population [Luo et al., 2005]. To elucidate the phylogeny of the *Triticum*–*Aegilops* alliance, Fourier transform infrared spectroscopy has been employed and revealed that *Ae. speltoides*, *Ae. speltoides* var. *aucheri*, and *Ae. speltoides* var. *ligustica* are close to each other but are on separate branches in the phylogenetic tree [Demir et al., 2015].

In several other papers in which *Aegilops* specimens were studied, they were catalogued as *Ae. aucheri* in botanical collections [Goncharov, Kononov, 1996; Goryunova et al., 2008; Belousova, Chikida, 2019].

After Kihara [1966] showed that *Ae. speltoides* or a closely related species was the maternal form in the first cross with diploid wheat, it has become possible to investigate relationships within the *Triticum*–*Aegilops* alliance by means of the maternal line via an analysis of their chloroplast and mitochondrial genomes (plasmon). In this context, interest in plastid DNA has increased.

Therefore, special attention should be paid to research articles on chloroplast DNA of *Triticum* and *Aegilops*. RFLP profiles of chloroplast DNA of some species of polyploid wheats of lineages *turgidum-aestivum* and *timopheevii-zhukovskiyi* — together with *Aegilops* from the section *Sitopsis* and some others — have been obtained; these data have led to the conclusion that *Ae. speltoides*, *Ae. bicornis*, or *Ae. sharonensis* could not have been a cytoplasmic donor for polyploid forms, but perhaps such a donor was *Ae. longissima* [Ogihara, Tsunewaki, 1982; Tsunewaki, Ogihara, 1983]. (It is now known that this is not the case.) Nonetheless, a more important conclusion was drawn by the authors about the *timopheevii-zhukovskiyi* lineage, namely that only *Ae. aucheri* has a profile identical to that of these polyploid wheats. Later, the same authors have done similar work and found that the RFLP profile of the chloroplast genome in *Ae. aucheri* and *Ae. speltoides* matches such a profile of wheats from the *timopheevii-zhukovskiyi* lineage [Ogihara, Tsunewaki, 1988]. Subsequently, K.Tsunewaki and colleagues have performed PCR-single-strand conformation polymorphism analysis on several fragments of chloroplast and mitochondrial genomes of many *Aegilops* taxa, including *Ae. speltoides* var. *auch.* and *Ae. speltoides* var. *ligust.* [Wang et al., 1997].

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Along with many species from the *Triticum*–*Aegilops* alliance, *Ae. speltoides* has been investigated, and the sequencing of fragments of its chloroplast genes yielded a phylogenetic tree on which this species is in the same clade as species of polyploid wheats of the timopheevii-zhukovskiy lineage, while hexaploid bread wheat and other species of the turgidum-aestivum lineage formed a separate clade [Golovnina et al., 2007]. A similar study has been fulfilled by other authors [Dizkirici et al., 2013], but they have not included representatives of timopheevii-zhukovskiy polyploid wheats in the analysis, and therefore their result has turned out to be ambiguous, although *Ae. speltoides* has been represented by several specimens: *Ae. speltoides* var. *aucheri* and *Ae. speltoides* var. *ligustica*.

In one of reviews in this field, four specimens of subspecies *Ae. speltoides ligustica* (1, 2) and *Ae. speltoides aucheri* (3, 4) were compared, and it was found that on the phylogenetic tree, some of them (2, 3) are closer to timopheevii-zhukovskiy, while others (1, 4) are closer to turgidum-aestivum [Tsunewaki, 2009]; this outcome can be explained by errors in their botanical description.

On the other hand, such data as nucleotide sequences of short fragments of the chloroplast genome cannot be compared with results from an analysis of nucleotide sequences of complete chloroplast genomes regarding accuracy of the construction of phylogenetic trees. It is now time to describe the current situation with the sequencing of complete chloroplast genomes of wheat taxa and their wild relatives, with a view to identifying donors of maternal subgenomes.

The complete plastid genomes of Triticeae including section Sitopsis and their relatives

The complete chloroplast genome of *T. aestivum* (Chinese Spring) was first sequenced in 2000 [Ogihara et al., 2000]. Its size was determined to be 134540 bp. It has later been found to be 134545 bp long [Ogihara et al., 2002]. The scientific community had to wait for more than 10 years for next complete chloroplast genomes from *Triticum* and *Aegilops*. Middleton et al. [2014] have sequenced 11 plastomes of diploid wheats *T. urartu*, *T. boeoticum*, and *T. monococcum*, two diploid *Aegilops* — potential donors of subgenomes of polyploid wheats — *Ae. speltoides* (S = B or G) and *Ae. tauschii* (D), as well as *Ae. cylindrica*, *Ae. geniculata*, rye *Secale cereale*, and two barley species: *Hordeum vulgare* and *H. spontaneum*. The size of their plastomes varied from 133444 to 136923 bp.

In the same year, 2014, the sequencing of 13 complete genomes of the following *Triticum* and *Aegilops* taxa was reported: *T. aestivum* ssp. *aestivum* cv. CS and ssp. *spelta*; *T. turgidum* ssp. *carthlicum*, ssp. *durum*, and ssp. *dicoccoides*; *Ae. speltoides* ssp. *ligustica* and ssp. *speltoides*; *T. timopheevii* ssp. *armeniicum*; *Ae. bicornis*; *Ae. searsii*; *Ae. sharonensis*; *Ae. longissima*; *Ae. kotschy*;

T. urartu; and *Ae. tauschii* [Gornicki et al., 2014]. The constructed phylogenetic tree suggested that the species and subspecies of *T. turgidum* and *T. aestivum* form a separate clade. At the same time, *Ae. speltoides* proved to be closer to *T. timopheevii*. Species *T. urartu* and *Ae. tauschii* were located between them and an *Aegilops* specimen from the subsection Emarginata, which turned out to be very distant from both polyploid wheat lineages. Meanwhile, *Aegilops* taxa from Emarginata together with *Ae. tauschii* ended up in a separate clade of the D lineage on the tree.

The following year, four complete plastid genomes of wheats from the Zanduri group were sequenced: *T. monococcum* var. *hornemanii*, *T. timopheevii*, *T. zhukovskiy*, and *T. araraticum* [Gogniashvili et al., 2015]. Analysis of the nucleotide sequences of these species revealed a high similarity of chloroplast genomes between *T. timopheevii* and *T. zhukovskiy*, which is not surprising because the former became a maternal form for the latter. The plastome of *T. araraticum* differed from that of *T. timopheevii* by a slightly greater number of substitutions and indels (insertions/deletions).

Bernhart et al. [2017] have compared complete chloroplast genomes of a number of Triticeae taxa, among them seven species of *Triticum* and five species from Emarginata, and from Truncata, there was *Ae. speltoides* (three specimens). On the phylogenetic tree, it was evident that all *Ae. speltoides* specimens are closer to the timopheevii-zhukovskiy lineage, whereas all species from Emarginata are far from *Ae. speltoides*.

A later comparison of complete chloroplast genomes of a relatively large number of species from the tribe Triticeae, including several major species of the *Triticum*–*Aegilops* alliance (excluding *aucheri* species/subspecies), again showed that *Ae. speltoides* is much closer to the timopheevii-zhukovskiy lineage than to turgidum-aestivum [Chen et al., 2020]. Those authors compared complete chloroplast genomes of several Triticeae species and constructed a phylogenetic tree in which the Emarginata branch was found to be adjacent to *Ae. tauschii*, while *Ae. speltoides* was on a separate branch with *Ae. speltoides* ssp. *ligustica* [Chen et al., 2021].

Among the 10 *Aegilops* and 15 *Triticum* species of interest to us, *Ae. longissima* and *Ae. tauschii* constitute a separate branch on the phylogenetic tree, just as *Ae. speltoides* together with *T. timopheevii* and *T. zhukovskiy* [Fu, 2021]. Moreover, this pattern was similar in cases where *S. cereale* or *H. vulgare* served as an outgroup.

In another study, a comparison of whole plastomes of Pooideae was made [Orton et al., 2021]. There, *Ae. longissima*, *Ae. sharonensis*, and *Ae. bicornis* (all Emarginata) together with *Ae. tauschii* (genome D) clustered into a group distant from polyploid wheats,

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whereas *T. speltoides* was closer to the timopheevii-zhukovskiy lineage than to turgidum-aestivum.

Elsewhere [Lubna et al., 2022], after sequencing of complete chloroplast genomes of *T. sphaerococcum* and *T. turgidum* ssp. *durum*, a phylogenetic tree was built using numerous *Triticum* and *Aegilops* species and showed that *Ae. speltoides*, *Ae. speltoides* var. *ligustica*, and *Ae. speltoides* var. *speltoides* are on neighboring branches of the same clade along with wheats of the timopheevii-zhukovskiy lineage, while the turgidum-aestivum lineage forms a sister clade. At the same time, *Ae. tauschii* is in a separate clade together with species from the subsection Emarginata [Lubna et al., 2022].

Consequently, the above results from comparisons of different *Triticum* and *Aegilops* species clearly indicate that *Aegilops* taxa from Emarginata are not donors of B and G subgenomes of polyploid wheats of both lineages. By contrast, previously, they have all been thought to be donors of B and G subgenomes in various years, as discussed in detail in a review by N.Haider [2013]. The donors of B and G subgenomes have most likely been two species from the subsection Truncata and one of them could theoretically also be *Ae. aucheri* or its relatives. Of course, it can be theorized that chloroplast genome B in the turgidum-aestivum lineage has undergone greater changes during evolution at the tetraploid level than genome G has in a younger timopheevii-zhukovskiy lineage as compared to its original donors with S genomes.

Phylogenetic tree of several species of Triticeae, including *Ae. aucheri*

We also recently sequenced several whole plastomes of wheats and *Aegilops* [Kuluev et al., 2024; 2024a; 2024b]. Our other article deals with five specimens of *Ae. aucheri* from different geographical locations (Kuluev et al., 2025, in press). A comparison of plastomes of *Ae. aucheri* with those of *Ae. speltoides* clearly indicates that they are different species. Later, we have sequenced two more specimens of *Ae. aucheri*, and now a phylogenetic tree is constructed with the help of MEGA 11 software [Tamura et al., 2021] for a few species of the section Sitopsis, *Ae. tauschii*, diploid wheats, and several species from lineages turgidum-aestivum and timopheevii-zhukovskiy (Fig. 3). The phylogenetic tree was generated under optimal model GTR+I+G, and statistical support was assessed through 1000 bootstrap replicates. As one can see in Fig. 3, it contains all the major species of the *Triticum*–*Aegilops* alliance, including those that have somehow participated in the formation of polyploid wheat lineages turgidum-aestivum and timopheevii-zhukovskiy, whose complete chloroplast genomes have been sequenced. *S. cereale* is an outgroup species. Just as in papers by other authors, species of the subsection Emarginata, together with *Ae. tauschii* and diploid wheats, represent a separate clade, divided into two branches 1.1 and 1.2: *Aegilops* (D) and diploid wheats (A).

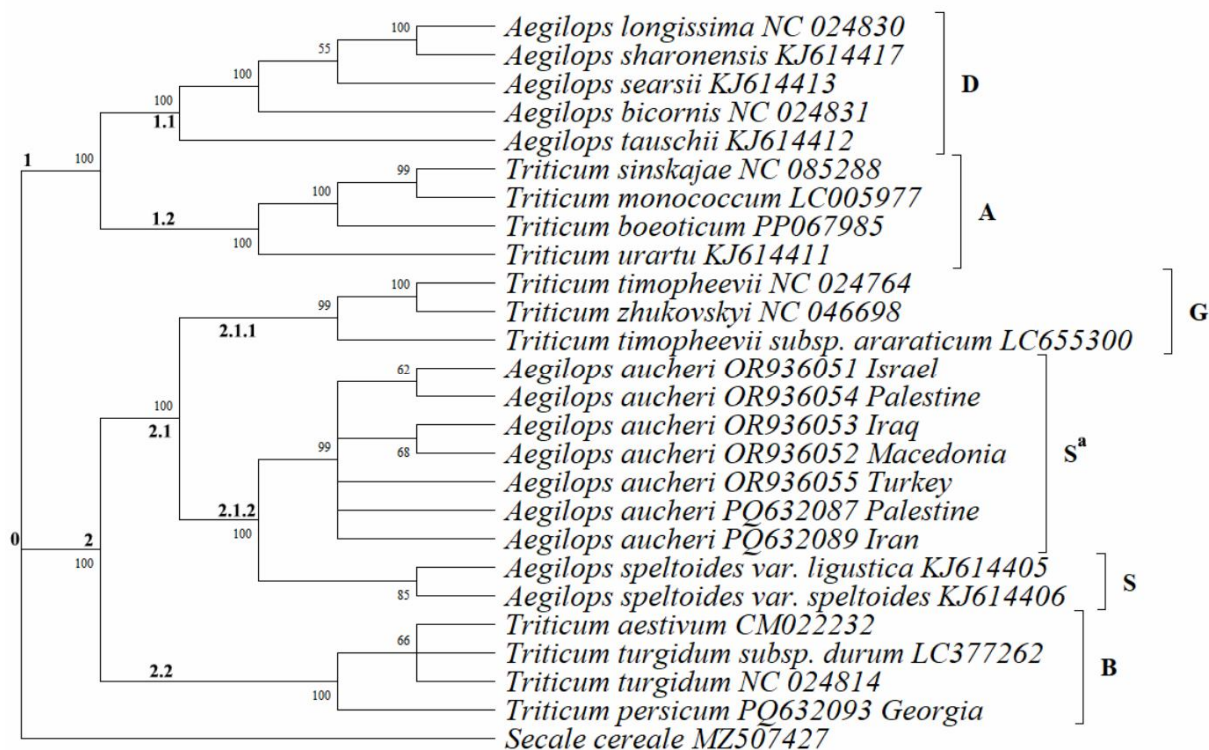


Fig. 3. The phylogenetic tree of several *Triticum* and *Aegilops* species on the basis of nucleotide sequences of their whole chloroplast genomes having GenBank accession numbers (further explanations are in the text).

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Another large clade (2) consists of polyploid wheat lineages *turgidum-aestivum* (B) and *timopheevii-zhukovskyi* (G) as well as two *Aegilops* species from the subsection *Truncata* that have S genomes: *Ae. speltoides* (var. *speltoides* and var. *ligustica*) and *Ae. aucheri*. The chloroplast genome of the latter species has been exclusively sequenced by us and is represented by specimens of different geographical origins. Their sizes vary within 135666 – 135668 bp among the accessions. This clade contains two branches 2.1 and 2.2, the most distant of which is that of *turgidum-aestivum*. This observation confirms other authors' conclusions mentioned above, namely that the currently known species (subspecies) of the subsection *Truncata* are closer to wheats having the subgenome G. Smaller branches are formed by wheats of the *timopheevii-zhukovskyi* lineage (2.1.1), *Ae. aucheri*, and two subspecies of *Ae. speltoides* (2.1.2). Furthermore, it can be assumed that *Ae. aucheri* is also close to donor of subgenome G as two variants of *Ae. speltoides*.

Taking into account the sequencing data of the complete plastid genomes of many *Triticum* and *Aegilops* species, the subsection *Truncata* because of its remoteness from the subsection *Emarginata*, as well as its importance for the evolution of wheat is need to give probably the status of at least a section or subgenus or even genus under names as *Sitopsis* or *Truncata*. A possible alternative is to remove the subsection *Emarginata* from *Sitopsis*, thereby leaving *Ae. speltoides* and *Ae. aucheri* in the latter. As for the subsection *Emarginata*, it should be included in the section *Vertebrata* as a subsection owing to the similarity of chloroplast genomes of these species to that of *Ae. tauschii*.

Conclusion

In the work mentioned above, Zhukovsky [1928] quoted prophetic words of Vavilov, who, in a personal conversation, said about the determination of the origin of polyploid wheats: "this problem is enough for 100 years." Indeed, Vavilov turned out to be right, because almost a century later, true donors of all subgenomes of both tetra- and hexaploid wheats of two lineages *turgidum-aestivum* and *timopheevii-zhukovskyi* are still unidentified.

Nevertheless, high-throughput sequencing of new generations has made it possible to sequence not only chloroplast but also nuclear genomes on a fairly large scale in plants, including *Triticeae* species, thus providing fundamentally new and important information. Complete chondriomes of *Triticum* and *Aegilops* are of lesser taxonomic interest because of their larger size than those of plastomes with the same matrilineal inheritance. As for the nuclear genomes, determination of their complete nucleotide sequences can shed additional light on the species that have served as paternal forms, but it is desirable to sequence their diploid (functionally, regardless of actual ploidy) genomes, and their phased

assembly of haplotypes had better be performed in T2T format. This is because quasi-genomes assembled in the usual manner now have a mosaic nature: they are composed of randomly interspersed fragments of maternal and paternal chromosomes, making such an analysis somewhat difficult. On the 100th anniversary of the term 'genome', we noted that the time for sequencing haploid genomes is coming to an end and the time for sequencing diploid genomes is already here [Kuluev et al., 2020]. To date, no phased genomes have been assembled for the *Triticum-Aegilops* alliance species, but there is no doubt that they will be soon, as such haplotype-resolved genomes are already known for more than 100 plants, including genomes with sizes even larger than those of wheats.

It is reasonable to expect that the donors of the wheat subgenomes, especially the maternal subgenomes B and G, will be identified in the coming years.

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